

24. M. Pagani, K. H. Freeman, N. Ohkouchi, K. Caldeira, *Paleoceanography* **17**, 1069 (2002).
25. P. Valentine, *Init. Rep. Deep Sea Drill. Proj.* **95**, 359 (1987).
26. K. G. Miller, W. A. Berggren, J. Zhang, J. A. A. Palmer, *Palaios* **6**, 17 (1991).
27. W. Wei, S. W. Wise, *Mar. Micropaleontol.* **14**, 119 (1989).
28. C. Pujol, *Init. Rep. Deep Sea Drill. Proj.* **72**, 623 (1983).
29. R. M. Leckie, C. Farnham, M. G. Schmidt, *Proc. Ocean Drill. Program* **130**, 113 (1993).
30. S. W. Wise Jr., *Init. Rep. Deep Sea Drill. Proj.* **71**, 481 (1983).
31. I. A. Basov, P. F. Ciesielski, V. A. Krashenninikov, F. M. Weaver, S. W. Wise Jr., *Init. Rep. Deep Sea Drill. Proj.* **71**, 445 (1983).
32. W. A. Berggren, D. V. Kent, C. C. I. Swisher, M. P. Aubry, in *Geochronology, Time Scales and Global Stratigraphic Correlation*, W. A. Berggren, D. V. Kent, M. P. Aubry, J. Hardenbol, Eds. (Special Publication No. 54, Society for Sedimentary Geology, Tulsa, OK, 1995), pp. 129–212.
33. N. J. Shackleton, M. A. Hall, A. Boersma, *Init. Rep. Deep Sea Drill. Proj.* **74**, 599 (1984).
34. Calculation of $\epsilon_{p37.2}$ requires knowledge of the $\delta^{13}\text{C}$ of ambient $\text{CO}_{2\text{aq}}$ ($\delta^{13}\text{C}_{\text{CO}_{2\text{aq}}}$) during alkenone production and of temperature, which can be approximated from the $\delta^{13}\text{C}$ of shallow-dwelling foraminifera, assuming isotopic and chemical equilibria among all the aqueous inorganic carbon species and atmospheric CO_2 , as well as foraminiferal calcite (17). In this study, records of planktonic foraminifera coeval with alkenone measurements were available from sites 511, 513, and 803. Site 612 had well-preserved planktonic and benthic foraminifera, but some samples lacked coeval samples of planktonic foraminifera. In these cases, the isotopic compositions of planktonic foraminifera were modeled by calculating the average difference between benthic and planktonic foraminifera and adding this value to the isotopic compositions of benthic foraminifera. Site 516 had poor carbonate preservation and lacked an adequate foraminiferal record. For this site, surface $\delta^{13}\text{C}_{\text{CO}_{2\text{aq}}}$ and values were modeled from the $\delta^{13}\text{C}$ compositions of the <60- μm fine fraction (FF), assuming an isotopic offset between the FF and shallow-dwelling foraminifera of $\pm 0.5\text{‰}$, as indicated by Miocene (50) and Eocene (this study) records from this site. Similarly, surface-water temperatures, required in the calculation of both $\delta^{13}\text{C}_{\text{CO}_{2\text{aq}}}$ and $p\text{CO}_2$, were estimated from the $\delta^{18}\text{O}$ compositions of shallow-dwelling planktonic foraminifera or modeled from the $\delta^{18}\text{O}$ compositions of the <60 μm FF, assuming an isotopic offset between the FF and shallow-dwelling foraminifera of -1.5‰ (50).
35. B. Rost, U. Riebesell, S. Burkhardt, *Limnol. Oceanogr.* **48**, 55 (2003).
36. J. Backman, J. O. R. Hermelin, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **57**, 103 (1986).
37. J. Young, *J. Micropaleontol.* **9**, 71 (1990).
38. J. Young, personal communication.
39. $\epsilon_{p37.2}$ is related to $[\text{CO}_{2\text{aq}}]$ by the expression $\epsilon_p = \epsilon_f - b/[\text{CO}_{2\text{aq}}]$, where ϵ_f represents the carbon isotope fractionation due to carbonxylation. b represents the sum of physiological factors, such as growth rate and cell geometry, affecting the total carbon isotope discrimination. In the modern ocean, b is highly correlated to surface-water $[\text{PO}_4^{3-}]$ (19). However, it is unlikely that $[\text{PO}_4^{3-}]$ alone is responsible for the variability in growth rate inferred from variation in b . Instead, $[\text{PO}_4^{3-}]$ may represent a proxy for other growth-limiting nutrients, such as specific trace elements that exhibit phosphate-like distributions.
40. For comparison with our record, middle to late Eocene estimates of ocean pH using the boron isotopic compositions of foraminifera (15) yield early Eocene CO_2 concentrations that are potentially 10 times higher than preindustrial levels (~ 3500 ppmv), reaching levels as low as ~ 350 ppmv during the middle to late Eocene. Our Eocene estimates do not support a scenario of low $p\text{CO}_2$ during this time.
41. T. E. Cerling *et al.*, *Nature* **389**, 153 (1997).
42. M. Pagani, K. H. Freeman, M. A. Arthur, *Science* **285**, 876 (1999).
43. R. W. Pearcy, J. Ehleringer, *Plant Popul. Biol.* **7**, 1 (1984).
44. M. D. Hatch, *Biochim. Biophys. Acta* **895**, 81 (1987).
45. J. R. Ehleringer, R. F. Sage, L. B. Flanagan, R. W. Pearcy, *Trends Ecol. Evol.* **6**, 95 (1991).
46. B. S. Gaut, J. F. Doebley, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 6809 (1997).
47. E. A. Kellogg, in *C₄ Plant Biology*, R. F. Sage, R. K. Monson, Eds. (Academic Press, New York, 1999), pp. 313–371.
48. D. L. Fox, P. L. Koch, *Geology* **31**, 809 (2003).
49. R. E. Sage, *New Phytol.* **161**, 341 (2004).
50. A. Ennyu, M. A. Arthur, M. Pagani, *Mar. Micropaleontol.* **46**, 317 (2002).
51. D. P. Schrag, *Chem. Geol.* **161**, 215 (1999).
52. P. N. Pearson *et al.*, *Nature* **413**, 481 (2001).
53. M. Pagani, M. A. Arthur, K. H. Freeman, *Paleoceanography* **15**, 486 (2000).
54. B. N. Popp, F. Kenig, S. G. Wakeham, E. A. Laws, R. R. Bidigare, *Paleoceanography* **13**, 35 (1998).
55. W. G. Mook, J. C. Bommerson, W. H. Staberman, *Earth Planet. Sci. Lett.* **22**, 169 (1974).
56. C. S. Romanek, E. L. Grossman, J. W. Morse, *Geochim. Cosmochim. Acta* **56**, 419 (1992).
57. J. Erez, B. Luz, *Geochim. Cosmochim. Acta* **47**, 1025 (1983).
58. B. N. Popp *et al.*, in *Reconstructing Ocean History: A Window into the Future*, F. Abrantes, A. Mix, Eds. (Plenum, New York, 1999), pp. 381–398.
59. M. E. Eek, M. J. Whiticar, J. K. B. Bishops, C. S. Wong, *Deep-Sea Res. II* **46**, 2863 (1999).
60. R. F. Weiss, *Mar. Chem.* **2**, 203 (1974).
61. All carbonates are assumed to be diagenetically altered to some degree, which acts to increase their $\delta^{18}\text{O}$ composition (51, 52), yielding minimum temperatures. In order to compensate for this uncertainty, three temperature estimates were used in the calculation of $\epsilon_{p37.2}$ and $p\text{CO}_2$, reflecting minimum temperatures calculated directly from the $\delta^{18}\text{O}$ value of carbonates (Temp_{min}), intermediate temperatures ($\text{Temp}_{\text{min}} + 3^\circ\text{C}$), and maximum temperatures ($\text{Temp}_{\text{min}} + 6^\circ\text{C}$).
62. K. H. Freeman, M. Pagani, in *A History of Atmospheric CO_2 and its Effects on Plants, Animals, and Ecosystems*, J. R. Ehleringer, T. E. Cerling, M. D. Dearing, Eds. (Springer, New York, 2005), pp. 35–61.
63. The authors thank two anonymous reviewers who helped improve the quality of the manuscript. We also thank B. Berner and K. Turekian for coffee and animated conversations that helped develop and inspire ideas. This work was funded by a grant from NSF.

21 January 2005; accepted 7 June 2005

Published online 16 June 2005;

10.1126/science.1110063

Include this information when citing this paper.

Global Mammal Conservation: What Must We Manage?

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We present a global conservation analysis for an entire “flagship” taxon, land mammals. A combination of rarity, anthropogenic impacts, and political endemism has put about a quarter of terrestrial mammal species, and a larger fraction of their populations, at risk of extinction. A new global database and complementarity analysis for selecting priority areas for conservation shows that $\sim 11\%$ of Earth’s land surface should be managed for conservation to preserve at least 10% of terrestrial mammal geographic ranges. Different approaches, from protection (or establishment) of reserves to countryside biogeographic enhancement of human-dominated landscapes, will be required to approach this minimal goal.

Research on population and species extinctions shows an accelerating decay of contemporary biodiversity. This pressing environmental problem is likely to become even worse in coming decades (1–3). Although impacts of human activities are global in scope, they are not uniformly distributed. The biota of certain countries and regions can be identified as being most at risk, having both exceptionally high

richness and endemism and exceptionally rapid rates of anthropogenic change. Because resources for conservation are limited, ecologists must provide managers and politicians with solid bases for establishing conservation priorities (4) to minimize population and species extinctions (5), to reduce conservation conflicts (6, 7), and to preserve ecosystem services (8).

Even for charismatic taxa, we lack a global view of patterns of species distributions useful for establishing conservation priorities. Such a view would allow evaluation of the effort required, for example, to preserve all species in a given taxon. It would also be relevant to setting global conservation goals such as protecting a certain percentage of Earth’s land surface (9). More restricted approaches such as identifying hot spots and endemic bird areas have called attention to relatively small areas where large numbers of species might be protected (10–13). For instance, recently the number of vertebrate species that lack populations within major protected areas was estimated (12). But now more comprehensive analyses are possible.

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Here we conduct a global examination of mammal distributions to evaluate conservation priorities based on (i) range size distribution, (ii) global patterns of species richness, (iii) political endemism (i.e., the proportion of species restricted to one country), (iv) the minimum area required to preserve one population or 10% of the range of each species, and (v) conservation conflicts in priority areas.

We created maps for 4795 mammal species, excluding only marine species, from the literature (14, 15). To evaluate the minimum area required for preserving these mammal species, we compared “minimal” and “conservative” preservation criteria. Under the minimal criterion, cells required to have appropriate management to preserve all mammal species in at least one 10,000-km² cell were selected. Under the conservative criterion, enough cells were selected to preserve a minimum of 10% of the range of each species. Using a percentage criterion was judged better than selecting a number of cells, because we are only dealing with conservation of species here. The much more difficult and possibly more important issue of population conservation to maintain ecosystem services (2) is only partially considered and obviously would require even more extensive management. Our selection of cells includes the complete distribution of many species with a species range (SR) equal to or smaller than 10,000 km², and a large percentage of the SR of species with a range smaller than 50,000 km². A database of cells and the species found in each was entered into the MARXAN Reserve Design program (version 1.8.2) (16) to produce 250 scenarios for both minimal and conservative preservation criteria (15). Each scenario was a result of MARXAN’s simulated annealing algorithm set to produce an optimal solution based on 10,000 iterations. We used the best solution (the one needing the minimum number of cells) to represent our global conservation management network (16). We used a fractional crop cover data set to estimate the proportion of each cell that is occupied by cropland (17). Spatially

referenced human population data from the Center for International Earth Science Information Network [CIESIN (18)] were used to determine the population density for each cell in the global reserve network.

Species with small geographic ranges are more vulnerable to human impacts (and thus to extinction) than are widespread ones, and the number of those restricted-range species is positively related to the number of sites re-

quired to preserve global mammalian diversity. Although the geographic distributions of land mammals vary from very small (<10 km²; one cell) for some island species to very large for species such as the wolf (*Canis lupus*, >49 million km²; 4900 cells), most (76%) species have a SR smaller than 1 million km² (100 cells) (Fig. 1). Rare species ($n = 1198$), defined here as those comprising the first quartile of the frequency distribution of geographic

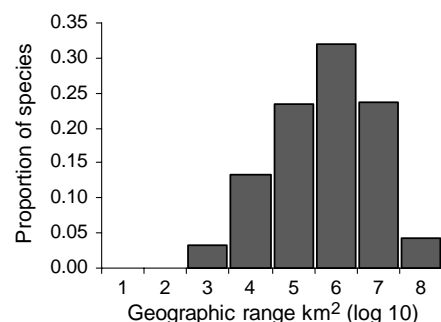


Fig. 1. Most mammal species have relatively small geographic ranges (<400,000 km²), encompassing 20% or less of the continent where they occur. Such limited geographic ranges tend to make those species relatively prone to extinction.

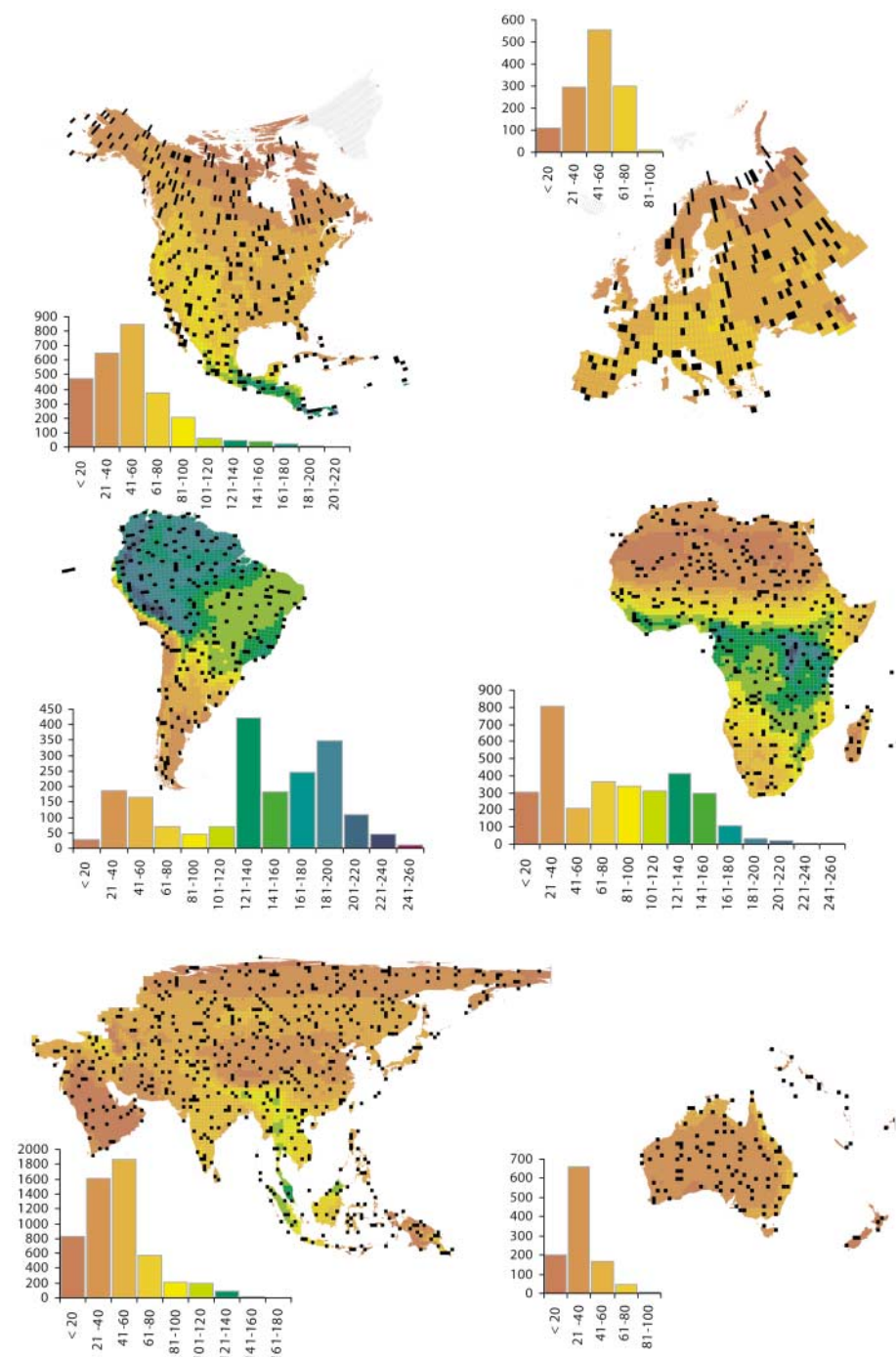


Fig. 2. Patterns of mammal species richness in six major regions of the world. The abscissa shows number of cells, and the ordinate shows species richness. Most diverse regions are found in South America and Africa. Marked cells indicate priority areas for the maintenance of 10% of the geographic ranges of all mammal species.

ranges, have a SR smaller than 24,000 km² (less than three cells, roughly half the size of Costa Rica). There are more rare species in Asia, followed by Africa, South America, North America, and Australia. Similarly, 32% (1531) of the species have a SR smaller than 50,000 km² (five cells), which is a threshold used with other factors to determine species endangerment by international conservation agencies such as the World Conservation Union (19). An unexpected result is that only 8% of mammal species are exclusively found in hot spots [sensu (11)], 62% are shared between hot spots and other regions [i.e., “cold spots” sensu (13)], and 30% are restricted to cold spots. Similarly, the ranges of 95% of all species intersect with at least one reserve in the 2004 IUCN/UNEP (World Conservation Union/United Nations Environment Programme) World database of protected areas.

As expected on the basis of biogeographic theory and patterns in other taxa, distribution of mammal species richness is very heterogeneous, with regions of low and high diversity on each continent and higher richness at lower latitudes (Fig. 2). As a result, the number of species in a single cell varies from 10 to 257. Most cells throughout the world have relatively few species (<100), especially in large regions in northern Africa and Asia, and nearly all of Europe and Australia. Unexpectedly, only four regions—Central America, the Andes-Amazonia in South America, east-central Africa, and Southeast Asia—have very rich cells, containing 200 or more species. South America has by far more of these cells.

The threat to the almost 40% (1900) of politically endemic (5) mammals is at least partially negatively correlated with economic

development. Developing nations often lack resources for conservation. Centers of political endemism, with 5% or more of the world's endemic mammals each, are Australia, Indonesia, Mexico, Brazil, the United States, Philippines, Madagascar, China, and Papua New Guinea. Most countries, and most megadiverse countries, are underdeveloped, and endemic species are concentrated in those countries. Some 47% (906) are found in countries like Iran, ranking below the top 100 countries in PPP (Purchase Parity Power; <U.S. \$5900); only 18% of mammal species are politically endemic to industrialized countries (PPP > U.S. \$11,000) (20).

The minimal preservation criterion (all species in at least one 10,000-km² cell) requires the management of 668 cells (6,680,000 km²), ~4.2% of Earth's ice-free land surface. In contrast, the more conservative criterion (cells to represent 10% of the geographic range of all species) requires managing at least 1702 cells (17,020,000 km²), accounting for 11% of the ice-free land surface. Cells in the conservative scenario were located in Asia (589), Africa (349), North America (299), South America (220), Europe (126), and Australia (119). Many mammal species (3293, 68%) were represented in very few priority cells (<10); 6% (290 species) were found in more than 100 cells, and the range was from 1 to 404 cells (Fig. 3). The total number of species occurrences in these cells, which could be used as a very conservative estimate for the number of populations [Mendelian populations or demographic units (2)] of mammals, is 116,103.

Practically, it is important to carry out a sensitivity analysis to determine the degree of substitutability of cells; that is, if one becomes

uninhabitable, how readily can a substitute be found. It is highly unlikely that all selected cells will retain high conservation value because human impacts and removing a degraded cell can affect the value of others in MARXAN scenarios. Hence, strategic conservation investment would involve back-up or next-best site sets as well as the priority set. More than 93% (15,057) of cells were selected in at least 1 of 250 scenarios for the 10% preservation criterion, and 135 cells (<1%) were irreplaceable, that is, selected in all scenarios (Fig. 2). Irreplaceable cells were located in all continents; most were in Asia (51, 37%), followed by North America (31, 23%), South America (20, 15%), Africa (19, 14%), Australia (10, 7%), and Europe (4, 4%). This is a favorable outcome, because 95% of the cells can be replaced by other cells without loss of conservation value, which gives the opportunity for strategic conservation planning. On the other hand, 1225 (72%) and 120 (89%) of the 1702 and 135 priority or irreplaceable cells in the best solution, respectively, intersect any one of the IUCN protected area polygons, indicating a relatively good correspondence between priority cells and protected areas.

To evaluate the extent to which a few species are driving the selection of priority cells, we quantified the difference in number of grid cells needed to achieve the conservative goal as compared to the number needed to protect 10% of the range of species endangered according to the IUCN (21). Only 48% (814) of cells would be required to represent those species, and those cells are found in North America (32%), Africa (27%), Asia (18%), South America (13%), Australia (8%), and Europe (2%). Similarly, we determined that to represent all mammals except rodents, the most diverse order, required 5% fewer cells. Randomly reducing the number of species to be protected at 10% intervals showed very slow reductions in the number of cells. Dropping 10, 20, 50, and 90% of the species represented a reduction of >1, 2, 7, and 21% of cells in the conservative (10%) representation goal.

Although land area under agriculture and human population density by themselves might seem to be crude estimators of anthropogenic impact, they actually are good indicators of overall biodiversity loss and conservation conflict, defined as the overlap of human activities and priority areas for conservation (22–26). We found a positive relation between species richness and human population density within the conservative, 10% criterion cells (Fig. 4A). One alarming result that requires immediate attention is that ~80% of the land area that must be managed under this conservative criterion has been affected to some degree by agriculture (Fig. 4B). Indeed, 20% of such cells have lost from 26 to 100% of their natural vegetation to agriculture, re-

Fig. 3. Frequency distribution of the number of cells occupied by mammal species in the conservative criterion, in which at least 10% of the range area of each species is protected. Most of these species occur in fewer than 40 100-km by 100-km cells, equivalent to the area of California (USA) or three-quarters the area of France.

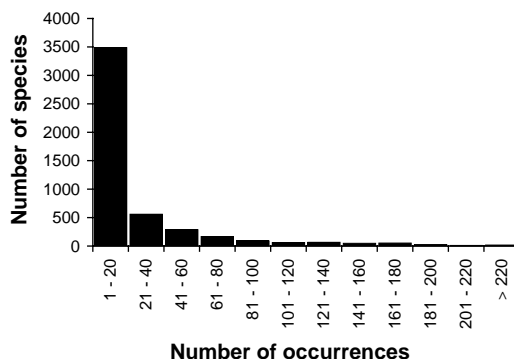
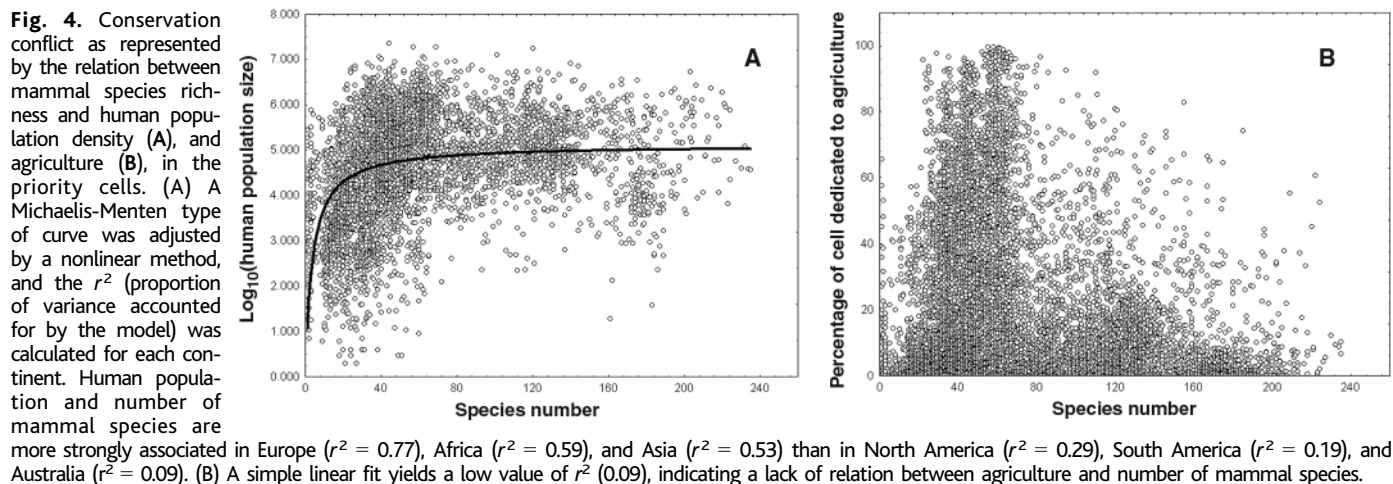


Table 1. Percentage of each priority cell for conservation covered by cropland (17) in six regions of the world. This is a measure of conservation conflict. Many cells have less than 25% conversion to cropland, suggesting opportunities for ameliorating conflict through countryside biogeography.

Cells	Africa	Asia	Australia	Europe	North America	South America	Total
None	20	14	55	6	36	1	20
1–25	70	58	39	35	41	95	59
26–50	6	13	5	29	14	4	11
51–75	4	11	1	22	6	0	7
76–100	0	4	0	8	3	0	3



ducing the value of each for conservation (Table 1).

Our results have clear implications for conservation. First, the large number of mammal species with restricted geographic ranges calls forth complex conservation scenarios because those species are intrinsically vulnerable to human impacts and stochastic extinction, and many are politically endemic. The high frequency of restricted ranges reinforces the obvious point that a larger and more dispersed selection of sites is required to preserve global mammalian diversity than would be required if range size distribution were skewed in the other direction. As the human population and its impacts have escalated, being politically endemic with a restricted geographic range in developing nations (e.g., orang-utan, *Pongo pygmeus*, in Indonesia) could, in most cases, considerably increase extinction risk because conservation legislation and resources are lacking. In contrast, the many endemic species in Australia are now subject to the kinds of intense management efforts that only rich nations are able to afford. Further complicating the conservation task is that even a well-known taxon such as mammals is more speciose than previously thought. There are now 10% more mammal species than were estimated a decade ago (27), and the total number is certain to be higher.

Second, our study supports previous ones showing that a large fraction of Earth's surface is important for the conservation of species diversity (9, 11, 12, 25). This is especially true given that we focus only on mammals—the cells that would be selected for, say, butterflies or freshwater fishes would likely be quite different (9). Obviously, it is very important to designate and manage reserves from which human activity is excluded or strongly restricted. Many species and populations such as the mountain gorilla (*Gorilla gorilla*) in Africa could not now survive without effective reserves. Conservation by pro-

tected areas, however, although effective and necessary, cannot be the only strategy. Even under optimistic assumptions, managing just 4% of Earth's surface, as in our minimum protection scenario, would be a gigantic task, especially when considering both high levels of conservation conflict throughout the world and gaps in the representation of species in protected areas.

In some places, the required habitat types or resources could be protected without formal reserves, through conservation finance approaches or through other cultural and political mechanisms. This work and related studies throw into sharp relief the importance of areas outside of protected parks and reserves for the maintenance of mammalian diversity. This is the domain of countryside biogeography (8). Many species can and do survive in regions with different degrees of human impact. For example, research in the Las Cruces region in southern Costa Rica indicates that a large percentage of the mammals (and other taxa) can survive in a region with ~9% of its original forest cover remaining (28). Similar patterns have been found throughout the world, even for populations of very large species such as tigers in India and Nepal (29). From the viewpoint of both ecosystem services and biodiversity preservation, we now need to start managing the whole planet better, as Vitousek *et al.* (30) point out. In some sense, “we” already manage the whole planet. However, the problem of planetary management, paying careful attention to “priority” grid cells and political endemism for a diverse selection of taxa, is especially daunting because of the great differences in the ability of nations to protect organisms within their borders. That, and the scale of the problem, mean that an unprecedented international effort will be needed—one requiring the development of both new attitudes and institutions (31). Developing those in a politically sensitive and cost-effective way is perhaps the major challenge for conservation biology.

References and Notes

1. P. R. Ehrlich, A. Ehrlich, *Extinction: The Causes and Consequences of the Disappearance of Species* (Random House, New York, 1981).
2. J. B. Hughes, G. C. Daily, P. R. Ehrlich, *Science* **278**, 689 (1997).
3. S. Pimm, P. Raven, *Nature* **403**, 843 (2000).
4. C. R. Margules, R. L. Pressey, *Nature* **405**, 243 (2000).
5. G. Ceballos, P. R. Ehrlich, *Science* **296**, 904 (2002).
6. W. G. Luck, G. C. Daily, P. R. Ehrlich, *Trends Ecol. Evol.* **18**, 331 (2003).
7. J. K. McKee, P. W. Sciulli, C. D. Foose, T. A. Waite, *Biol. Conserv.* **115**, 161 (2004).
8. G. C. Daily, Ed., *Nature's Services* (Island Press, Washington, DC, 1997).
9. T. M. Brooks *et al.*, *Bioscience* **54**, 1081 (2004).
10. A. J. Long, M. J. Crosby, A. J. Stattersfield, D. C. Wege, *Global Ecol. Biogeogr. Lett.* **5**, 281 (1996).
11. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, *Nature* **403**, 853 (2000).
12. A. S. Rodrigues *et al.*, *Nature* **428**, 640 (2004).
13. P. Kareiva, M. Marvier, *Am. Sci.* **91**, 344 (2003).
14. Supporting online material includes additional information on materials and methods, a list of all sources used for obtaining the distribution maps, and the list of species included in this study.
15. The maps are an approximation of the current geographic distributions of these species. Maps for well-known species such as lions are probably more accurate than are those for poorly known species of rodents, shrews, and bats. Maps were digitized and the data analysis was done using ArcView 3.3. Earth's surface was divided into a 10,000-km² grid cell network using the Behrmann equal area projection. We defined a species range (SR) as all cells that intersected the species map (32). We choose not to have a different threshold for species with tiny ranges, because our selection of 10,000 km² priority cells includes all or most of the range of species with a SR equal to or smaller than 10,000 km². A similar trend occurs for other species with other small SRs. For example, a single-cell representation of species with a 20,000- or 30,000-km² SR likely represents 50 and 33% of its geographic range, and so on.
16. H. I. Possingham, I. Ball, S. Andelman, in *Quantitative Methods for Conservation Biology*, S. Ferson, M. Burgman, Eds. (Springer, New York, 2000), pp. 291–305.
17. N. Ramankutty, J. A. Foley, *Glob. Ecol. Biogeogr.* **8**, 381 (1999).
18. <http://sedac.ciesin.columbia.edu/plue/gpw>
19. World Conservation Union (IUCN), *The 2003 IUCN Red List of Threatened Species* (IUCN, Gland, Switzerland, 2003).
20. World Bank, *World Development Indicators 2004* (World Bank, Washington, DC, 2004).
21. We considered as “endangered” all species classified by the 2003 IUCN red data list as critically endangered, endangered, and threatened (19).
22. J. Liu, G. C. Daily, P. R. Ehrlich, G. W. Luck, *Nature* **421**, 530 (2003).

23. A. Balmford *et al.*, *Science* **291**, 2616 (1991).
24. R. P. Cincotta, J. Wisniewski, R. Engelman, *Nature* **404**, 990 (2000).
25. K. J. Gaston, T. M. Blackburn, K. K. Goldewijk, *Proc. R. Soc. London B. Biol. Sci.* **270**, 1293 (2003).
26. D. Tilman *et al.*, *Science* **292**, 281 (2001).
27. A. Duff, A. Lawson, *Mammals of the World: A Checklist* (A & C Black, London, 2004).
28. G. C. Daily, G. Ceballos, J. Pacheco, G. Suzan, A. Sánchez Azofeja, *Conserv. Biol.* **17**, 1 (2003).
29. E. Wikramanayake *et al.*, *Conserv. Biol.* **18**, 839 (2004).
30. P. M. Vitousek, H. A. Mooney, J. Lubchenco, J. M. Melillo, *Science* **277**, 494 (1997).
31. P. R. Ehrlich, A. H. Ehrlich, *One with Nineveh: Politics, Consumption, and the Human Future* (Island Press, Washington, DC, 2004).
32. Environmental Systems Research Institute (ESRI), *ESRI Data and Maps 2002* (Environmental Systems Research Institute, Redlands, CA, 2002); see www.esri.com.
33. We thank G. C. Daily, R. A. Medellín, C. Sekercioglu, R. List, and K. M. A. Chan for comments on the manuscript. This study was supported by the National University of Mexico, CONABIO (Mexico), the Center for Conserva-

tion Biology—Stanford University, EcoCiencia (Mexico), and the John Simon Guggenheim Memorial Foundation.

Supporting Online Material
www.sciencemag.org/cgi/content/full/309/5734/603/DC1
Materials and Methods
References
Species list

25 April 2005; accepted 17 June 2005
10.1126/science.1114015

On the Regulation of Populations of Mammals, Birds, Fish, and Insects

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A key unresolved question in population ecology concerns the relationship between a population's size and its growth rate. We estimated this relationship for 1780 time series of mammals, birds, fish, and insects. We found that rates of population growth are high at low population densities but, contrary to previous predictions, decline rapidly with increasing population size and then flatten out, for all four taxa. This produces a strongly concave relationship between a population's growth rate and its size. These findings have fundamental implications for our understanding of animals' lives, suggesting in particular that many animals in these taxa will be found living at densities above the carrying capacity of their environments.

The way a population's size changes through time—its dynamics—depends on the way it grows when small and declines when big. More specifically, the dynamics result from the precise relationship between the population's size (N) and its per capita growth rate (pgr), defined as $1/N \times dN/dt$, where t is time (Fig. 1). The simplest case is a straight-line relationship, such that pgr declines linearly with increasing N (Fig. 1A, left). Linearity produces the well-known logistic population growth equation $N(t) = \frac{KN_0}{(K - N_0)e^{-r_0 t} + N_0}$, where r_0 is a parameter representing pgr when $N = 0$, N_0 is the size of the population at time $t = 0$, and K is the population's carrying capacity (I).

The relationship between pgr and N is generally taken to be monotonic and decreasing and can be either concave or convex (2). Convex relationships (Fig. 1B) imply that pgr varies little until population size is near carrying capacity, then drops rapidly. Concavity (Fig. 1C) means that pgr is initially relatively high, so small populations grow quickly, but pgr then declines rapidly as

population size increases, later flattening out so that the approach to carrying capacity is relatively slow. In a variant possible in theory and occasionally reported in nature, the slope of the relationship between pgr and N becomes positive in small populations, such that pgr actually increases with N over a narrow range of population sizes, giving an Allee effect (2–4).

The way in which pgr declines with population size is conventionally modeled by the theta-logistic equation, given by

$$pgr = r_0[1 - (N/K)^\theta] \quad (1)$$

where r_0 and K are as before, and θ is a parameter describing the curvature of the relationship (2). In practice, population density is sometimes used in place of population size, and r_0 is best replaced by r_m , representing pgr when population size N is at a defined low value, corresponding to a population of, for example, one individual (5) (Fig. 2). Values of θ greater or less than 1 correspond to convex and concave relationships, respectively (Figs. 1 and 2). Mechanistically, the value of θ must depend on the ways that animals interact at different densities (6).

There has been a persistent suggestion that the shape of the pgr -density relationship depends on a species' life history (5, 7, 8). The widely cited argument (9–14) is as follows. Large, long-lived species generally live close to

the carrying capacity of their environments, being limited mainly by resources, and are only rarely subject to natural selection for increased performance at low population density. As a consequence, these species' population growth rates are relatively unaffected until populations are nearing carrying capacity, producing the convex curve of $\theta > 1$ seen in Fig. 1. By contrast, species that spend most of their time at densities much lower than carrying capacity are selected for a high maximum rate of increase. As a result, these species are affected even at relatively low densities in their abilities to acquire foods, and so the concave relationship of $\theta < 1$ between pgr and N arises. There are a number of cases of density dependence that together have suggested that pgr -density relationships are convex for large mammals and similar species but concave for species with life histories like those of insects and some fish (5, 7, 15).

The form of the pgr -density relationship has implications beyond population dynamics, and it is used to make predictions and to analyze management options in areas such as conservation (16), pest management (17), risk assessment (18), and disease epidemiology (19). In spite of this, there have been few attempts to establish generalities about how pgr varies with population size (5, 15, 20). Here we analyze an extensive compilation of time series data from 4926 different populations in the Global Population Dynamics Database (GPDD) (21, 22). The GPDD is a collection of time series of population counts or indices of these, together with other taxonomic details of more than 1400 species.

After exclusion of time series that were very short, did not vary, or contained zeros, the GPDD contained 3766 time series from 1084 species (table S1). We further excluded 469 series (12%) that showed a significant decline in size with time, because unknown factors may have prevented population recovery and biased the form of the estimated pgr -density relationship, and 1% that showed positive density dependence (i.e., pgr increased with density), because these show no evidence of population regulation. We examined the remaining 3269 series for evidence of Allee relationships, but these were rare if present at all: There were only 20 cases in which a quadratic regression of pgr on N fitted better ($P < 0.05$) than a linear regression, with a turning point of the required

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